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DIURNAL VARIATIONS OF PHOTOSYNTHETIC RATES AND XYLEM PRESSURE POTENTIALS IN FOUR DWARF SHRUBS (ERICACEAE) IN AN ALPINE ZONE

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Abstract: Microenvironments, net photosynthetic rates and xylem pressure potentials (XPP) were measured for four evergreen dwarf shrubs (Ericaceae) co-existing under the edge of a *Pinus pumila* canopy in the alpine region of Mt. Norikura on August 13, 1991. The day was clear till about 12 p.m., frequent fog set in the afternoon. When the leaves were directly exposed to sunlight, their temperature and leaf-to-air vapor pressure deficit (VPD) increased to about 40°C and 0.06 Pa Pa^{-1}, respectively. Leaf temperature and VPD were less in the afternoon when there was fog. The diurnal changes of net photosynthetic rate showed two peaks in early morning and afternoon, when leaf temperature and VPD were low. *Gaultheria pyroloides, Phyllodoce aleutica* and *Vaccinium vitis-idaea* took on greater amounts of carbon during the morning than the afternoon, while the reverse was noted for *Rhododendron aureum. V. vitis-idaea* had less carbon gain per unit leaf area during the daytime. The carbon gain per dry mass of aerial productive-parts (sum of leaf and stem) did not differ among species, since *V. vitis-idaea* had a large leaf area ratio. Minimum XPP during the daytime in *P. aleutica* and *V. vitis-idaea* was lower than in the other two species. *V. vitis-idaea* especially showed osmotic adjustment and had ridged cell walls. This species did not, thus, have lower diurnal turgor potential or lower relative water content (RWC) compared with the other species. *R. aureum* and *G. pyroloides* with high XPP during daytime did not show osmotic adjustment, and had elastic cell walls.

1. Introduction

Alpine plants live in an environment generally described as cold and windy, with snow cover, a short growth period and reduced partial pressure of O_2 and CO_2 consequent to decrease in atmospheric pressure (*e.g.* BILLINGS and MOONEY, 1968; LARCHER, 1983; BLISS, 1985; FRIEND and WOODWARD, 1990). Although early studies on alpine plants described plant communities and floristics (COOPER, 1908; RYDBERG, 1914; HOLM, 1927; COX, 1933), recent attempts have been made to consider ecophysiological traits of plants and their environment together to explain their distribution (*e.g.* MOONEY, 1963; MOONEY and JOHNSON, 1965; BILLINGS and MOONEY, 1968; KNAPP *et al.*, 1989). Some evidence that some alpine plants have evolved in response to their particular environment has been found in recent studies.

The environment in alpine regions is characterized by not only severity but

also fluctuation. Short-term variations in sunlight characterized by alternating periods of full sun and shade are common in mountainous regions (EVANS, 1956; WOODS and TURNER, 1971; YOUNG and SMITH, 1979, 1983; CHAZDON and FETCHER, 1984; KNAPP and SMITH, 1988, 1989; KNAPP *et al.*, 1989). Plants growing in alpine regions are exposed to both high temperature and evaporation demand in intense solar radiation, and low radiation and evaporation demand in fog. KNAPP and SMITH (1988, 1989) and KNAPP *et al.* (1989) compared the response of photosynthetic rates and stomatal conductances to fluctuating sunlight for some subalpine herbs. Differences in the small-scale distribution patterns of two subalpine herbs, *Arnica cordifolia* and *Arnica latifolia*, could be related to the degree of exposure to continuous full sunlight and their respective capabilities for withstanding short-term periods of extremely high evaporative demand (YOUNG and SMITH, 1979).

The diurnal changes in microenvironment, xylem pressure potentials of shoots and photosynthetic rates were measured for four co-occurring evergreen dwarf shrubs, Ericaceae, in the same habitat in an alpine region of central Japan on a summer day. The present study was conducted to determine (1) the differences of responses among co-occurring species in photosynthetic rate and water relations to fluctuating sunlight, and (2) the relationships between the ecophysiological traits in water use and carbon gain and the pressure-volume characteristics.

2. Materials and Methods

2.1. Study site and materials

The study was carried out in an alpine area on Mt. Norikura, in Hida mountains, in central Japan (36°06′N, 137°33′E, alt. 2850 m). Mean annual temperature was −2.4°C and warmth and coldness indices, 13.4 and 102.7°C Month, respectively, from 1982 to 1989 (climate data from the Norikura Solar Observatory). Mean air temperature and precipitation in August were 11.3°C and 304 mm, respectively, from 1982 to 1989. The frequency of clear sky was 41.3% at 9 a.m. and 17.3% at 3 p.m., and the frequency of foggy and cloudy sky was 43.3% at 9 a.m. and 63.9% at 3 p.m. in August from 1982 to 1989. Soil of the study stand is volcanic origin. The study site was on the east-facing slope in the stand. The snow-free season is about June to November at this stand. Dwarf pine, *Pinus pumila* (PALLAS) REGEL, covers a rock-free area in the stand. The canopy height is about 40 cm. Some dwarf cushion-forming species co-existed under the edge of the *P. pumila* canopy. The shoot heights of cushion plants were less than 20 cm. Current shoots elongated from July in these species. Leaf expansions was finished by September. Four major species, *Gaultheria pyroloides* HOOK. et THOMS., *Phyllodoce aleutica* (SPRENG.) A. HELLER, *Rhododendron aureum* GEORGI and *Vaccinium vitis-idaea* L., were chosen from cushion plants. The study site was 40 cm toward the open area from the edge of the *P. pumila* canopy. All species were evergreen shrubs of Ericaceae. Another major species in the stand was *Empetrum nigrum* L. var. *japonicum* K. KOCH, Empetraceae.

2.2. Field surveys

Microclimatological measurements were made on August 13, 1991. The data were stored every minute in data-loggers (THERMODAC-E, Eto-Denki Co. Ltd., Tokyo, Japan). Ambient air temperature (T_{air}) at the canopy height and leaf temperature (T_{leaf}) were measured with fine-wire copper constantan thermocouples (diameter: 0.1 mm, Hayasi-Denko Co. Ltd., Tokyo, Japan). T_{leaf} was measured with thermocouples attached to the abaxial leaf surface by adhesive tape. Photosynthetically active photon flux density (PPFD ; μmol m^{-2} s^{-1}, 400–700 nm of wave length) was determined with a quantum sensor (IKS-25, Koito-Kogyo, Co. Ltd., Tokyo, Japan) placed over the canopy. Relative humidity (RH) was measured with a thin-film capacitance sensor (HMD-30Y, Vaisala Inc., Helsinki, Finland) placed on the canopy. An aluminum roof was fixed above the humidity sensor to prevent direct solar radiation. Atmospheric pressure was 71 kPa on this day.

An ecophysiological study was made while taking microclimatological data. For *G. pyroloides, P. aleutica* and *V. vitis-idaea*, ecophysiological data were obtained from current year shoots. For *R. aureum*, measurement was made for current year leaves. The diurnal time variations of net photosynthetic rate and total vapor conductance (stomatal and cuticular conductance) of current year shoots in each species were measured with an H_2O/CO_2 portable porometer (Li-6200, Li-Cor Inc., Nebraska, U.S.A.). Xylem pressure potential (XPP) in each species was determined with a Scholander-type pressure bomb (PMS-600, Plant Moisture Stress Inc., Oregon, U.S.A.) immediately after cutting off shoots or leaves (SCHOLANDER *et al.*, 1965).

2.3. Laboratory experiments

Aerial shoots were collected on August 16, 1991. They were divided into flower, bud, leaf, and stem organs. The leaf area was measured with an area meter (Li-3000, Li-Cor Inc., Nebraska, U.S.A.). Each organ was then dried at 80°C and weighed.

To determine differences in the bulk modulus of elasticity and osmotic potential at full turgor among species, three pressure-volume (PV) curves were obtained for shoots of each species. Experiments were conducted using current year shoots of *G. pyroloides, P. aleutica* and *V. vitis-idaea*, and current year leaves of *R. aureum*. All shoots were collected on August 16, 1991 and fully rehydrated by covering them with polyethylene bags for more than 12 hours under dark and moist conditions. They were subsequently dehydrated at room temperature. XPP decreased in steps of about 0.2 MPa. The leaf area and dry mass of each sample were measured after obtaining PV curves. Water-saturated leaf mass in each sample was extrapolated using the linear regression function of XPP to fresh leaf mass. Changes in relative shoot water content (RWC) were determined from water-saturated shoot mass and average fresh mass before and after measurements of XPP by the following equation (MARUYAMA and MORIKAWA, 1983).

$$\text{RWC}=(\text{average fresh mass} - \text{dry mass})/(\text{water-saturated fresh mass} - \text{dry mass}). \quad (1)$$

The bulk modulus of elasticity (ε) in cell walls was determined by linear regression between turgor potential (Ψp) and RWC. The regression fitted the phase at which Ψp sharply decreased with decrease in RWC. The shoot capacitance (C) was calculated by the following equation.

$$C=(\text{water-saturated fresh mass} - \text{dry mass})/\varepsilon. \quad (2)$$

3. Results

3.1. Microclimate

The day was clear in the morning and frequently foggy in the afternoon. PPFD exceeded 2500 μmol m^{-2} s^{-1} in the morning (Fig. 1a). PPFD peaked at about 12 p.m. and then decreased with fluctuation due to fog in the afternoon (Fig. 1a). RH decreased with the increase in PPFD and T_{air} in the morning, and increased with fluctuation due to fog in the afternoon (Fig. 1b). Maximum T_{leaf} values of *G. pyroloides, P. aleutica, R. aureum* and *V. vitis-idaea* were 35.6, 34.5, 40.4 and 40.2°C, respectively, in the morning. Maximum leaf to air

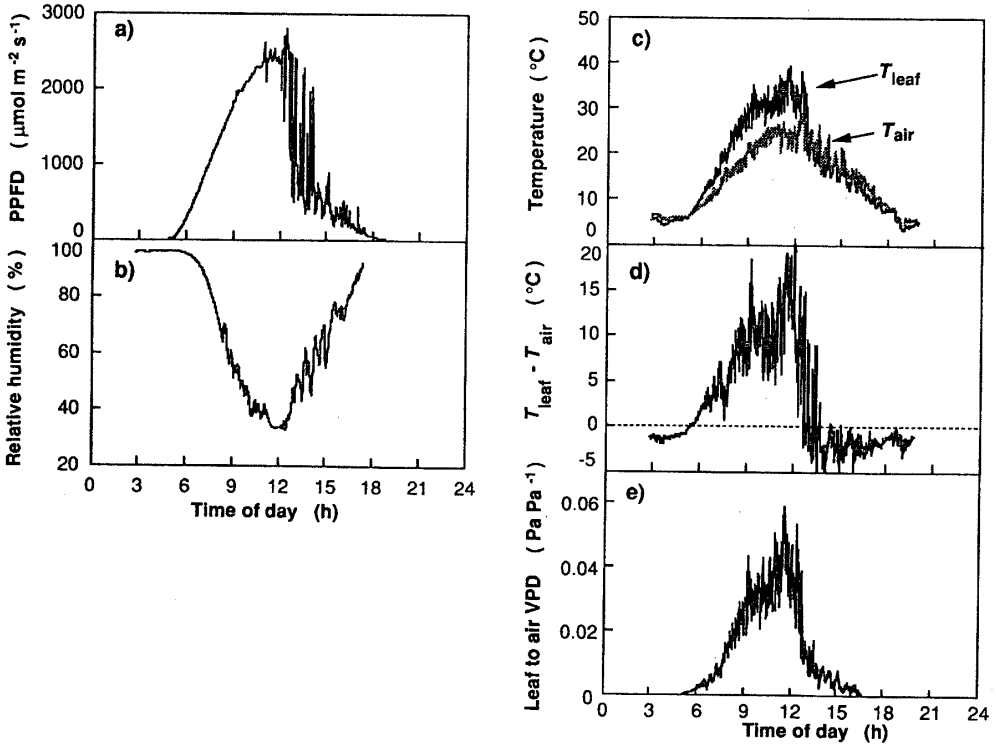

Fig. 1. Diurnal patterns of microclimates on August 13, 1991: (a) photosynthetically active photon flux density (PPFD), (b) relative humidity (RH), (c) ambient air temperature (T_{air}) and leaf temperature (T_{leaf}) in Rhododendron aureum, *(d) difference of air temperature with leaf temperature in R. aureum, (e) leaf-to-air vapor pressure deficit (VPD) in* R. aureum.

temperature differences of *G. pyroloides, P. aleutica, R. aureum* and *V. vitis-idaea* were 12.2, 11.0, 19.9 and 19.9°C, respectively, in the morning. Leaf temperature in the afternoon was less than air temperature for all species. Leaf-to-air vapor pressure deficit (VPD) increased with the decrease in RH and increase in T_{leaf} in the morning. A sudden decrease in VPD due to fog was noted in the afternoon (Fig. 1e).

3.2. *Photosynthesis*

Maximum net photosynthetic rates of *G. pyroloides, P. aleutica, R. aureum* and *V. vitis-idaea* in the morning were 13.3, 11.2, 7.7 and 6.5 μmol m^{-2} s^{-1}, respectively. Net photosynthetic rates in *G. pyroloides* and *P. aleutica* peaked from 7 to 8 a.m. and, in *R. aureum* and *V. vitis-idaea*, from 8 to 9 a.m. (Fig. 2). Net photosynthetic rates showed a second peak during the afternoon in all species. The first peak in the morning was higher than the second peak in the afternoon in *G. pyroloides* and *P. aleutica*. In *R. aureum* and *V. vitis-idaea*, first and second peak values were essentially the same (Fig. 2).

V. vitis-idaea had the lowest net CO_2 gain per unit leaf area during the daytime, 0.144 mol m^{-2} (Table 1). Net CO_2 gain per unit dry mass of aerial productive-parts (leaf and stem, excluding flower and fruit) during the daytime did not, however, differ among the species, owing to the high leaf area ratio (the ratio of leaf area to dry mass of aerial productive-parts) of *V. vitis-idaea*. The percentages of net CO_2 gain during the morning to total diurnal net CO_2 gain were 84.1, 68.8, 45.1 and 82.6 % in *G. pyroloides, P. aleutica, R. aureum* and *V. vitis-idaea*, respectively.

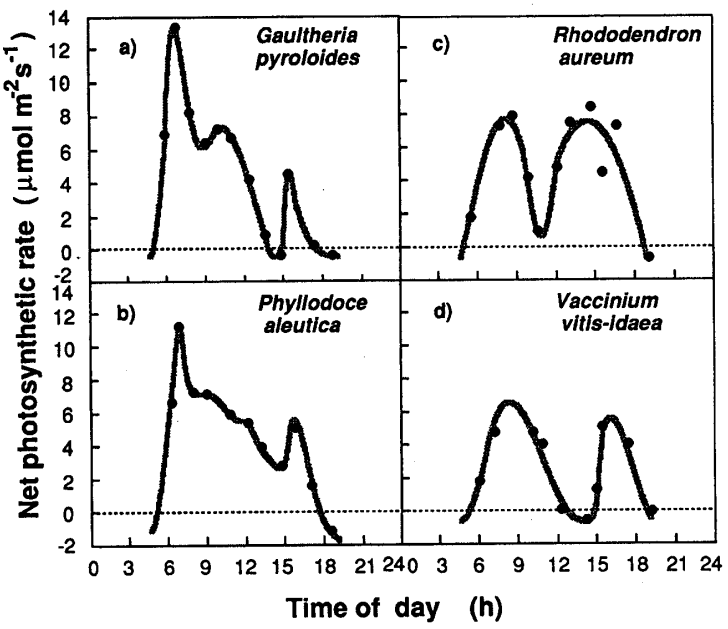

Fig. 2. Diurnal patterns of net photosynthetic rates of a) G. pyroloides, *b)* P. aleutica, *(c)* R. aureum, *(d)* V. vitis-idaea *on August 13, 1991. Bold lines are visually fitted curves.*

Table 1. Net carbon gain per unit leaf area and per unit productive-part (P-part) dry mass of aerial shoot in daytime, August 13, 1991. Leaf area ratio per unit P-part dry mass in aerial shoots shows morphological characteristics of aerial shoots in each species examined.

	Gaultheria pyroloides	*Phyllodoce aleutica*	*Rhododendron aureum*	*Vaccinium vitis-idaea*
Net carbon gain per until leaf area (mol m^{-2} $daytime^{-1}$)	0.222	0.228	0.245	0.144
Net carbon gain per unit P-part dry mass (mmol g^{-1} $daytime^{-1}$)	1.13	1.17	1.11	1.25
Leaf area ratio of P-part dry mass in aerial shoots ($\times 10^{-3}$ $m^2 g^{-1}$)	5.09	5.13	4.53	8.69
Ratio of net carbon gain in the morning to net carbon gain in the daytime (%)	84.1	68.8	45.1	82.6

3.3. *Water relations*

V. vitis-idaea and *P. aleutica* showed lower osmotic potential at full turgor, (−1.79 and −1.57 MPa respectively), than other species (Fig. 3 and Table 2). *R. aureum* indicated the highest osmotic potential at full turgor, −1.38 MPa. XPP at the turgor loss point of *R. aureum* was the least (−2.08 MPa). That of *P. aleutica* was the highest (−1.80 MPa). For *V. vitis-idaea* and *P. aleutica*, larger bulk modulus of elasticity in cell walls (ε) was noted (33.3 and 22.2 MPa,

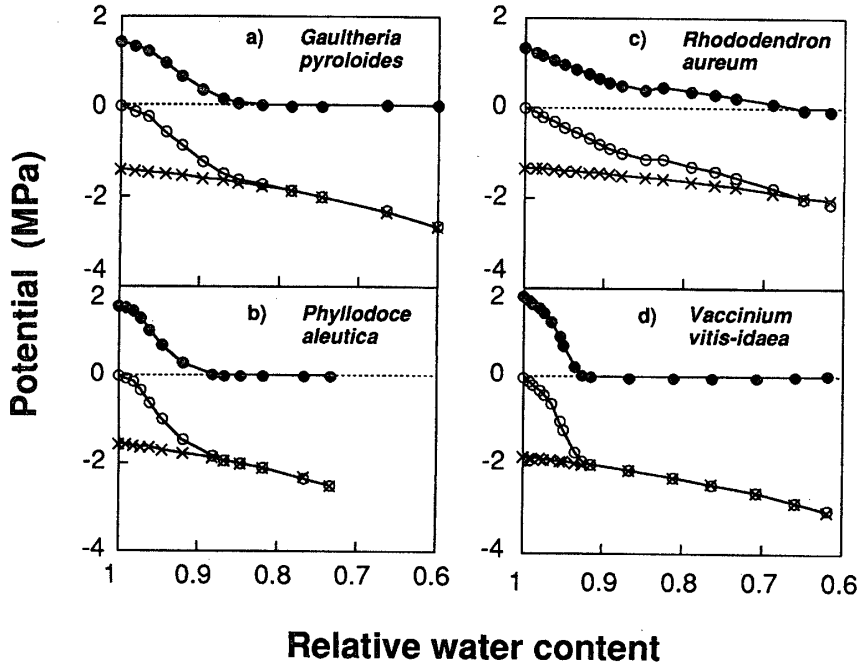

Fig. 3. Relationships of xylem pressure potentials (○), turgor potentials (●) and osmotic potentials (×) to relative water content of shoots (RWC) determined from PV curves in a) G. pyroloides, *b)* P. aleutica, *(c)* R. aureum, *(d)* V. vitis-idaea *on August 16, 1991.*

Table 2. Osmotic potential at full turgor, xylem pressure potential at turgor loss point, bulk modulus of elasticity in cell walls, and capacitance of shoots examined on August 16, 1991.

	Gaultheria pyroloides	*Phyllodoce aleutica*	*Rhodopdendron aureum*	*Vaccinium vitis-idaea*
Osmotic potential at full tugor (MPa)	−1.40	−1.57	−1.38	−1.79
Xylem pressure potenitial at turgor loss point (MPa)	−1.89	−1.80	−2.08	−1.99
Bulk modulus of elasticity in cell walls; ε (MPa)	12.2	22.2	7.0	33.3
Capacitance of shoot ; C (mol m^{-2} MPa^{-1})	0.40	0.21	1.41	0.14

respectively) and shoot capacitance (C) was smaller (0.14 and 0.21 mol m^{-2} MPa^{-1}, respectively).

P. aleutica and *V. vitis-idaea*, having lower osmotic potential at full turgor and larger bulk modulus of elasticity in cell walls, showed lower XPP in the daytime (Fig. 4). Minimum XPP during the daytime in each species was recorded at about 8 a.m. for *P. aleutica, R. aureum* and *V. vitis-idaea* (Fig. 4). Gently decreasing in the morning, XPP in *G. pyroloides* was smallest at about 9:30 a.m. The XPP changes during fogginess in the afternoon were the same for all species.

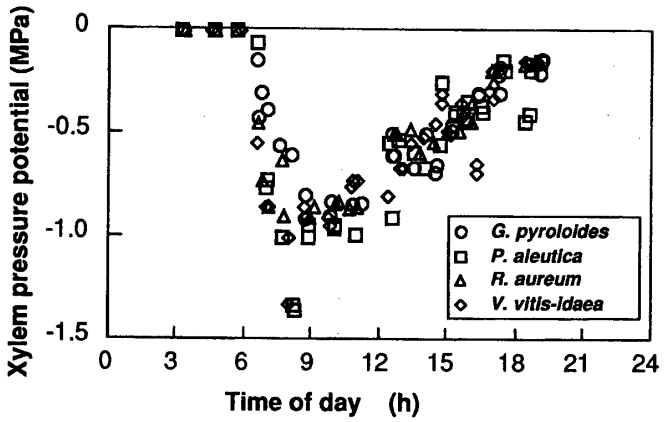

Fig. 4. Diurnal changes of xylem pressure potential (XPP) in the four species on August 13, 1991.

Figure 5 shows diurnal changes in turgor potential and RWC determined from diurnal patterns in XPP in Fig. 4 and PV curves in Fig. 3. Although XPP of *P. aleutica* and *V. vitis-idaea* was lower in the morning than that of the other two species (Fig. 4), the estimated turgor potential of *V. vitis-idaea* was not lower. Estimated diurnal RWC of *P. aleutica* and *V. vitis-idaea* was higher than that of the other two species.

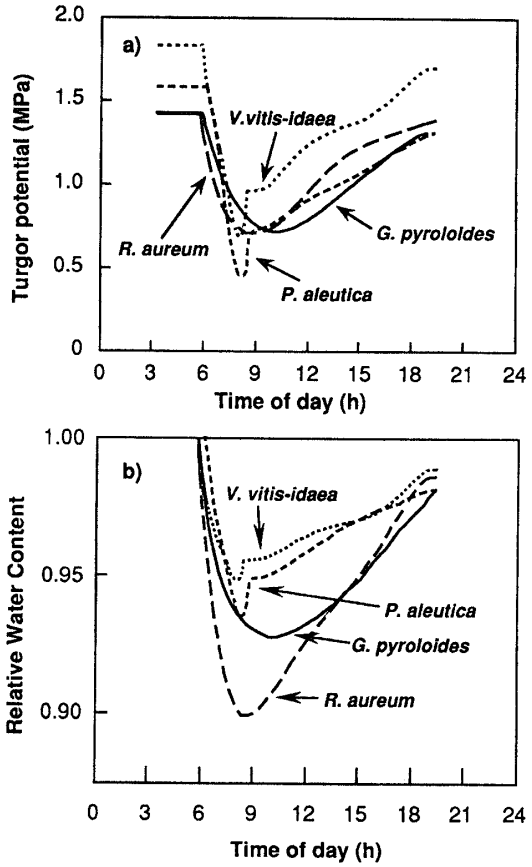

Fig. 5. Diurnal changes in turgor potential and relative water content (RWC) estimated from diurnal patterns of xylem pressure potential indicated in Fig. 4 and PV curves shown in Fig. 3.

4. Discussion

4.1. Microclimate

High leaf-to-air vapor pressure deficit (VPD) and leaf temperature (T_{leaf}) caused severe dehydration in dwarf shrubs in alpine regions, when leaves were exposed to direct radiation on a summer day (Fig. 1). Alpine cushion plants (SPOMER, 1964; SALISBURY and SPOMER, 1964) and alpine rosette plants (SCHULZE *et al.*, 1983) in Europe and Africa have also shown high VPD and T_{leaf}. These VPD and T_{leaf} values were equivalent to those observed in plants in dry environments such as desert and chaparral (ULMANN *et al.*, 1985; SMITH and OSMOND, 1987; NIELSEN *et al.*, 1990), Mediterranean (LANGE *et al.*, 1985; TENHUNEN *et al.*, 1987) and grass steppe (MONSON *et al.*, 1986).

Fog often sets in in alpine regions on summer days in central Japan. Fog was a major environmental factor in suppressing T_{leaf} and VPD of plants in the alpine region (Fig. 1). In this study, when direct radiation was prevented by fog in the afternoon, RH increased and T_{leaf} and VPD decreased in all the species. T_{leaf} and VPD of alpine plants under foggy conditions were basically the same as those of understory plants in cool temperate regions (YOUNG and SMITH, 1979; ISHIDA *et al.*, 1992).

4.2. Photosynthesis

Net photosynthetic rates in all species decreased at midday (Fig. 2). Stomatal closures and decreases in net photosynthesis rate with increase in VPD have been observed in some plants in alpine regions (SCHULZE *et al.*, 1985; KÖRNER and COCHRANE, 1985). Optimum leaf temperatures for photosynthetic rate are relatively low in many alpine plants (BILLINGS and MOONEY, 1968; LARCHER, 1973; PISEK *et al.*, 1973; SLATYER, 1978). The optimum leaf temperature of photosynthesis in *Loiseleuria cetrariosum*, evergreen dwarf shrub of Ericaceae in the Alps, has been observed to be about 10 to 15°C (GRABHERR and CERNUSCA, 1977). High T_{leaf} and VPD under non-foggy conditions during the daytime may be sufficient to depress net carbon gain.

There were two peaks for net photosynthetic rates in all species: 1) early morning before T_{leaf} and VPD became high, and 2) afternoon when fog caused decreases in T_{leaf} and VPD (Fig. 2). There were two types of diurnal patterns of net photosynthetic rates among the four species studied. *G. pyroloides, P. aleutica* and *V. vitis-idaea* took on larger amounts of carbon in the morning than in the afternoon, while *R. aureum* did so in the afternoon (Table 1) and was thus more capable of using foggy conditions for carbon gain.

KARLSSON (1989) compared carbon gains per unit leaf mass throughout the growing season for plants growing together in a subarctic region of Sweden. The carbon gain during the growing season did not significantly differ between two co-occurring evergreen dwarf shrubs, *Vaccinium vitis-idaea* and *Empetrum hermaphoroditum*. In this study, *V. vitis-idaea* showed lower net carbon gain per unit leaf area than that of other species during the daytime (Table 1). The amount of fixed carbon per unit dry mass of aerial productive-part was, however, essentially the same for all four species, since the leaf area ratio of *V. vitis-idaea* was the largest (Table 1). The morphological characteristics of aerial shoots in *V. vitis-idaea*, thus, compensated for the low net carbon gain per unit leaf area. It may be important for co-existence among species that the plants in a same habitat gain the same amounts of carbon.

4.3. Water relations

V. vitis-idaea and *P. aleutica*, whose XPP was low in the morning due to direct solar radiation, showed not only large bulk modulus of elasticity in cell walls but low osmotic potential at full turgor (Fig. 4 and Table 2). The same phenomenon has been reported for species growing in a cool temperate forest, that is, species with low XPP in daytimes had rigid cell walls and low osmotic potential at full turgor (ISHIDA *et al.*, 1992). In plants with rigid cell walls, XPP drops rapidly as a result of slight shoot dehydration without direct energy consumption (SALLEO, 1983), and large decrease in RWC does not occur with reduction in XPP (ISHIDA *et al.*, 1992). These species exhibited high RWC because of their rigid cell walls, even when XPP decreased considerably (Figs. 4 and 5).

Plants maintain their turgor potential by having low osmotic potential at full turgor. This is referred to as osmotic adjustment (TURNER and JONES, 1980).

ROBICHAUX (1984) hypothesized that this is of significant potential benefit in terms of diurnal turgor maintenance in some Hawaiian plants. In the present study, the diurnal turgor potential of shoots was maintained in all species and the variation among species in turgor potential was less than that in RWC of shoots (Fig. 5). Diurnal turgor maintenance may thus be important. However, *P. aleutica*, having the lowest XPP and turgor potential in the morning under direct exposure to sunlight, showed no effective osmotic adjustment. This indicates weak drought tolerance in this species. The distribution of *P. aleutica* is biased toward mesic stands, such as snow-bed sites, in alpine regions of Japan (MIZUNO, 1986, 1990).

R. aureum showed clearly different water relations and diurnal changes of net photosynthetic rate from the other three species. This species had low bulk modulus of elasticity in cell walls and large capacitance compared with the other species (Fig. 4 and Table 2). Apparent osmotic adjustment was not noted in *R. aureum* (Table 2). Although RWC of *R. aureum* largely decreased with the decrease in XPP, turgor potential was maintained because of the large capacitance (Fig. 5 and Table 2). Water relations in *R. aureum* with more elastic water storage shoots show the function of water conservation. The water use efficiency (the ratio of net photosynthetic rate to transpiration rate) in *R. aureum* during the afternoon was greater than that in the other three species (data not presented).

5. Conclusions

Although the diurnal changes in net photosynthetic rate and XPP differed among four co-occurring species in this alpine zone, the amounts of diurnal carbon gain per unit dry mass of aerial productive-parts was essentially the same for all species. *V. vitis-idaea* compensated low carbon gain per unit leaf area by having high leaf area ratio. Not only physiological but also morphological traits of plants determined their dry matter production. The dry matter production might made sure of co-occurring of plants.

XPP of *V. vitis-idaea* and *P. aleutica* largely and sharply decreased in the clear morning. These species had leaves which can withstand low XPP, because of having ridged cell walls and showing osmotic adjustment. These species took on larger amounts of carbon in the morning in direct sunlight than in the foggy afternoon. On the other hand, XPP of *R. aureum* and *G. pyroloides* did not, sharply and largely decreased in the morning, in contrast to the former two species. These species had leaves with elastic cell walls and did not show obvious osmotic adjustment. Although *R. aureum* showed greater carbon gain in the foggy afternoon than in the morning, *G. pyroloides* did so in the morning. Further studies are needed to determine the physiological traits which cause the differences in diurnal changes of net photosynthetic rate between these two species.

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References

BILLINGS, W. D. and MOONEY, H. A. (1968): The ecology of arctic and alpine plants. Biol. Rev., **43**, 481–529.

BLISS, L. C. (1985): Alpine. Physiological Ecology of North American Plant Communities, ed. by B. F. CHABOT and H. A. MOONEY. New York, Chapman and Hall, 41–65.

CHAZDON, R. L. and FETCHER, N. (1984): Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. J. Ecol., **72**, 553–564.

COOPER, W. S. (1908): Alpine vegetation in the vicinity of Long's Peak, Colorado. Bot. Gaz., **45**, 319–337.

COX, D. F. (1933): Alpine plant succession on James Peak, Colorado. Ecol. Monogr., **3**, 300–372.

EVANS, G. C. (1956): An area survey method of investigating the distribution of light intensity in woodlands. J. Ecol., **44**, 391–428.

FRIEND, A. D. and WOODWARD, F. I. (1990): Evolutionary and ecophysiological response of mountain plants to the growing season environment. Adv. Ecol. Res., **20**, 59–124.

GRABHERR, G. and CERNUSCA, A. (1977): Influence of radiation, wind, and temperature on the CO_2 gas exchange of the alpine dwarf shrub community *Loiseleurietum cetrariosum*. Photosynthetica, **11**, 22–28.

HOLM, H. T. (1927): Vegetation of the alpine region of the Rocky Mountains of Colorado. Natl. Acad. Sci. Mem., **3**, 1–45.

ISHIDA, A., YAMAMURA, Y. and HORI, Y. (1992): Roles of leaf water potential and soil-to-leaf hydraulic conductance in water use by understorey woody plants. Ecol. Res., **7**, 213–223.

KARLSSON, P. S. (1989): *In suit* photosynthetic performance of four coexisting dwarf shrubs in relation to light in a subarctic woodland. Funct. Ecol., **3**, 481–487.

KNAPP, A. K. and SMITH, W. K. (1988): Effect of water stress on stomatal and photosynthetic responses in subalpine plants to cloud pattern. Am. J. Bot., **75**, 851–858.

KNAPP, A. K. and SMITH, W. K. (1989): Influence of growth form and water relations on stomatal and photosynthetic responses to variable sunlight in subalpine plants. Ecology, **70**, 1069–1082.

KNAPP, A. K., SMITH, W. K. and YOUNG, D. R. (1989): Importance of intermittent shade to the ecophysiology of subalpine herbs. Funct. Ecol., **3**, 753–758.

KÖRNER, CH. and COCHRANE, P. M. (1985): Stomatal responses and water relations of *Eucalyptus pauciflora* in summer along an elevational gradient. Oecologia, **66**, 443–455.

LANGE, O. L., TENHUNEN, J. D. and BEYSCHLAG, W. (1985): Effects of humidity during diurnal courses on the CO_2- and light-saturated rate of photosynthetic in the sclerophyllous leaves of *Arbutus unedo*. Oecologia, **67**, 301–304.

LARCHER, W. (1973): Ökologie der Pflanzen. Stuttgult, Ulmer, 403 p.

LARCHER, W. (1983): Ökophysiologische Konstitutionseigenschaften von Gebirgspflanzen. Ber. Dtsch. Bot. Ges., **96**, 73–85.

MARUYAMA, Y. and MORIKAWA, Y. (1983): Ha no suibun-tokusei no sokutei, P-V kyokusen-hô (Measurement of leaf water relations using the pressure-volume technique). Nihon Ringaku-

kai Shi (J. Jpn. For. Soc.), **65**, 23–28.

MIZUNO, K. (1986): Daisetsu Zan nanbu Tomuraushi Yama shûhen no yôgan-daichi-jô ni okeru kôzan shokubutsu gunraku no ricchi jôken (Vegetation pattern in relation to environments on the lava plateaus around Mt. Tomuraushi in the southern part of the Daisetsu Mountains, Hokkaido). Chirigaku Hyôron (Geogr. Rev. Jpn.), **59** (Ser. A), 449–469.

MIZUNO, K. (1990): Alpine vegetation pattern in relation to environmental factors in Japanese high mountains. Tokyo Metropolitan University, DSc Thesis.

MONSON, R. K., SACKCHEWSKY, M. R. and WILLIAMS, G. J., III (1986): Field measurements of photosynthesis, water-use efficiency, and growth in *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4) in Colorado shortgrass steppe. Oecologia, **68**, 400–409.

MOONEY, H. A. (1963): Physiological ecology of coastal, subalpine and alpine populations of *Polygonum bistortoides*. Ecology, **44**, 812–816.

MOONEY, H. A. and JOHNSON, A. W. (1965): Comparative physiological ecology of an arctic and an alpine population of *Thalictrum alpinum* L. Ecology, **46**, 721–727.

NIELSEN, E. T., SHARIFI, M. R., RUNDEL, P. W., FORSETH, I. N. and EHLERINGER, J. R. (1990): Water relations of stem succulent trees in north-central Baja California. Oecologia, **82**, 299–303.

PISEK, A., LARCHER, W., VEGIS, A. and NAPP-ZIN, K. (1973): The normal temperature range. Temperature and Life, ed. by H. PRECHT *et al.* Berlin, Springer, 102–194.

ROBICHAUX, R. H. (1984): Variation in the tissue water relations of two sympatric Hawaiian *Dubautia* species and their natural hybrid. Oecologia, **65**, 75–81.

RYDBERG, P. A. (1914): Formation of the alpine zone. Bull. Torrey Bot. Club, **41**, 457–474.

SALLEO, S. (1983): Water relations parameters of two Sicilian species of *Senecio* (Groundsel) measured by the pressure bomb technique. New Phytol., **95**, 179–188.

SALISBURY, F. B. and SPOMER, G. G. (1964): Leaf temperatures of alpine plants in the field. Planta, **60**, 497–505.

SCHULZE, E.-D., BECK, E., SCHEIBE, R. and ZIEGLER, P. (1985): Carbon dioxide assimilation and stomatal response of afroalpine giant rosette plants. Oecologia, **65**, 207–213.

SCHOLANDER, P. F., HAMMEL, H. T., BRADSTREET, E. D. and HEMMINGSEN, E. A. (1965): Sap pressure in vascular plants. Science, **148**, 339–346.

SLATYER, R. O. (1978): Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sie. ex Spreng. VII. Relationship between gradients of field temperature and photosynthetic temperature optima in the Snow Mountains area. Aust. J. Bot., **26**, 111–121.

SMITH, S. D. and OSMOND, C. B. (1987): Stem photosynthesis in a desert ephemeral, *Eriogonum inflatum*. Morphology, stomatal conductance and water-use efficiency in field populations. Oecologia, **72**, 533–541.

SPOMER, G. G. (1964): Physiological ecology studies of alpine cushion plants. Physiol. Plant., **17**, 717–724.

TENHUNEN, J. D., HARLEY, P. C., BEYSCHLAG, W. and LANGE, O. L. (1987): A model of net photosynthesis for leaves of the sclerophyll *Quercus coccifera*. Functional analysis in Mediterranean ecosystems. Plant Response to Stress, ed. by J. D. TENHUNEN *et al.* Berlin, Springer, 339–354.

TURNER , N. C. and JONES, M. M. (1980): Turgor maintenance by osmotic adjustment: A review and evaluation. Adaptation of Plants to Water and High Temperature Stress, ed. by N. C. TURNER and P. J. KRAMER. New York, J. Wiley, 87–103.

ULMANN, I., LANGE, O. L., ZIEGLER, H., EHLERINGER, J., SCHULZE, E.-D. and COWAN, I. R. (1985): Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia. Oecologia, **67**, 577–587.

YOUNG, D. R. and SMITH, W. K. (1979): Influence of sunflecks on the temperature and water relations of two understory congeners. Oecologia, **43**, 192–205.

YOUNG, D. R. and SMITH, W. K. (1983): Effect of cloudcover on photosynthesis and transpiration in the subalpine understory species *Arnica latifolia*. Ecology, **64**, 681–687.

WOODS, D. B. and TURNER, N. C. (1971): Stomatal response to changing light by four tree species of

WOODS, D. B. and TURNER, N. C. (1971): Stomatal response to changing light by four tree species of varying shade tolerance. New Phytol., **70**, 77–84.

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